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Telemetry reveals limited exchange of walleye between Lake Erie and Lake Huron: Movement of two populations through the Huron-Erie corridor

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ABSTRACT

Immigration and emigration of individuals among populations influence population dynamics and are important considerations for managing exploited populations. Lake Huron and Lake Erie walleye (*Sander vitreus*) populations are managed separately although the interconnecting Huron-Erie Corridor provides an unimpeded passageway. Acoustic telemetry was used to estimate inter-lake exchange and movement within St. Clair River and Detroit River. Of 492 adult walleyes tagged and released during 2011 and 2012, one fish from Tittabawassee River (Lake Huron; 1 of 259, 0.39%) and one individual from Maumee River (Lake Erie; 1 of 233, 0.43%) exchanged lakes during 2011–2014. However, both fish returned to the lake where tagged prior to the next spawning season. The one walleye from Maumee River that moved to Lake Huron made repeated round-trips between Lake Erie and Lake Huron during three consecutive years. Of twelve fish tagged in the Tittabawassee River detected in the Huron-Erie Corridor, few (n = 3) moved south of Lake St. Clair to the Detroit River. Ten walleye tagged in the Maumee River entered the Huron-Erie Corridor, and five were detected in the St. Clair River. Our hypothesis that walleye spawning in Maumee River, Lake Erie, served as a source population to Lake Huron ("sink population") was not supported by our results. Emigration of walleye to Lake Huron from other populations than the Maumee River, such as those that spawn on in-lake reefs, or from Lake St. Clair may contribute to Lake Huron walleye populations.

Introduction

Movements are an important component of the life history of many fish species and play an important role in the distribution and abundance of fish populations across space and time. Understanding movement is especially important for fishery managers when populations exchange individuals through immigration and emigration across jurisdictional or management zone boundaries (Brenden et al., 2015; Cooke et al., 2016). Failure to account for contributions from multiple populations in harvest can lead to overexploitation of less productive populations or specific segments of a population (Larkin, 1977; Ying et al., 2011). Determination of exchange rates of individuals among populations can identify self-sustaining 'source' populations where reproduction exceeds mortality and thus can contribute to other adjacent populations, and to 'sink' populations that persist only because of immigration from source populations (Hanski, 1999). Identification of source-and-sink populations are important for determining the stock composition of mixed stock-fisheries, prioritization of conservation efforts for populations, and establishing spatially relevant management units and protected areas (Rooker et al., 2014; Zuccarino-Crowe et al., 2016). Source-sink dynamics require "permanent" exchange of individuals from one population to another and although source-sink dynamics has informed management of

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marine fish species (Crowder et al., 2000; Fogarty and Botsford, 2007), less is known about exchange of individuals among populations in large interconnected freshwater lakes, such as the Laurentian Great Lakes.

Walleye (*Sander vitreus*) populations in lakes Huron and Erie are the largest in the Great Lakes and support valuable recreational and commercial fisheries (Fielder and Bence, 2014; Roseman et al., 2010; Vandergoot et al., 2019). Prior to 1940, Saginaw Bay was the epicenter of the Lake Huron walleye fishery but overfishing, pollution, habitat degradation, and establishment of invasive species caused the fishery to fail (Fielder and Baker, 2019; Schneider and Leach, 1977). Collapse of non-native alewife (*Alosa psuedoharengus*) in 2003 coincided with increased walleye recruitment and an expansion of the Saginaw Bay walleye fishery (Fielder et al., 2007). Cessation of walleye stocking programs occurred in 2006, and walleye recovery goals for Saginaw Bay were met in 2009 (Fielder and Baker, 2019; Johnson et al., 2015). The estimated number of adult walleye (age 2 and older) in Saginaw Bay ranged from 2 to 4.5 million fish during 2006–2011 (Fielder and Bence, 2014).

Lake Erie walleye populations have fluctuated historically and underwent a sharp decline after 1950 due to overfishing and habitat degradation (Schneider and Leach, 1977; Vandergoot et al., 2019). Commercial walleye fisheries in most waters of Lake Erie were closed in 1970 due to human consumption concerns prompted by high levels of mercury in walleye flesh, but recreational fisheries later reopened in 1973 after mercury concentrations declined (Schneider and Leach, 1977). The number of age 2 or older walleye in the western and central basins of Lake Erie ranged from 20 to 40 million fish during 2010–2015 (Vandergoot et al., 2019; Walleye Task Group, 2016).

The Huron-Erie Corridor connects Lake Huron and Lake Erie and is the primary source of water to Lake Erie. The Huron-Erie corridor extends for 130 km through the industrial and urban landscapes of Detroit, Michigan and Windsor, Ontario, and provides an unimpeded migratory corridor for population exchange between lakes Huron and Erie (Fig. 1). The St. Clair River, Detroit River, and Lake St. Clair combine to form the Huron-Erie Corridor. In addition to providing a migratory link between lakes Huron and Erie, the Huron-Erie Corridor provides important spawning habitat for walleye and other large river spawning species such as lake sturgeon (*Acipenser fulvescens*) and lake whitefish (*Coregonus clupeformis*) (Hondorp et al., 2014; Manny et al., 2007). Lake St. Clair also supports a walleye population and has multiple spawning sites for this species.

Movement of walleye between Lake Huron and Lake Erie via the Huron-Erie Corridor is well documented although direct estimates of population-specific exchange are not known (Ferguson and Derksen, 1971; McParland et al., 1999; Todd and Haas, 1993; Wolfert, 1963). In a study of 93,670 adult walleye tagged in the Tittabawassee River (Lake Huron) during 1981–2011, jaw-tagged walleye were recovered throughout the Huron-Erie Corridor and western Lake Erie (Fielder, 2014). Analyses of temporal patterns in tag recoveries were stratified by two time periods characterized by lower densities of predominately stocked fish in Saginaw Bay (1981–2003) and higher density of wild fish (2006–2011) (Fielder, 2014), although the percentage of walleye that moved from the Tittabawassee River to the Huron-Erie Corridor was not calculated by Fielder (2014). Movement of walleye from the Tittabawassee River to Lake Huron was influenced by fish sex, size, and population density, and more jaw-tagged walleye from the Tittabawassee River were reported by anglers in the Detroit River and Lake Erie during 1981–2002 than 2006–2011 (Fielder, 2014). Similar tagging studies conducted on Lake Erie suggested movement of walleye is population specific. Jaw-tagged walleye released in the western basin of Lake Erie near Monroe, Michigan showed a strong tendency to move northward to Lake Huron through the Huron-Erie Corridor, with 23–38% of tags recovered annually from the Detroit River, Lake St. Clair, or Lake Huron during 1978–1987 (Todd and Haas, 1993).

The results described above stand in contrast to those from Vandergoot and Brenden (2014) where a spatially explicit population model was used to estimate the percentage of walleye that moved from Lake Erie to the Huron-Erie Corridor. Results of this study suggested a small percentage (<11%) of walleye tagged in western Lake Erie moved into the Huron-Erie Corridor or continued into Lake Huron between 1990 and 2007 (Vandergoot and Brenden, 2014). Similarly, a small percentage (3–6%) of externally tagged juvenile walleye released along the southern shore of western Lake Erie were recovered by anglers in the Detroit River between 1960 and 1962 (Wolfert, 1963). These mark-recapture studies estimated exchange of walleye based on recovery of tagged fish in recreational or commercial fisheries but may have been biased by heterogeneous spatial and temporal fishing effort.

Using various genetic markers, contributions of walleye from Lake Erie to commercial fisheries in the Ontario waters of southern Lake Huron were estimated to be 60–70% from fish harvested in 1994–1995 (McParland et al., 1999). Genetic mixed-stock analyses suggested 26% of walleye harvested during 2008–2009 in Saginaw Bay originated from Lake Erie or Lake St. Clair (Brenden et al., 2015). These genetic mixed-stock analyses were limited by the levels of genetic differentiation among potential source populations. Recent dramatic changes in the Lake Huron food web, specifically declines of alewife and rainbow smelt (*Osmerus mordax*) (Fielder and Baker, 2019) may have influenced exchange rates of walleye between lakes Huron and Erie. As a result of the studies reviewed above, the contribution of Lake Erie walleyes from various sources to either the Huron-Erie Corridor or Lake Huron widely ranged from 3% to 70%.

Our objective was to directly estimate exchange between a Lake Huron and a Lake Erie population based on movement of walleye through the Huron-Erie Corridor, independent of fishery recaptures. Spatio-temporal movement patterns were characterized by acoustic transmitters implanted in walleye and detected by the basin-wide Great Lakes Acoustic Telemetry Observation System (GLATOS – http://glatos.glos.us/) network of receivers (Krueger et al., 2018). We determined the percentage of walleye tagged in the Maumee River in Lake Erie that moved to Lake Huron through the Huron-Erie Corridor and the percentage of walleye tagged in the Tittabawassee River in Lake Huron that moved to Lake Erie through the Huron-Erie Corridor. As well, we characterized the multi-year movement patterns of walleye detected in the Huron-Erie Corridor. Our expectation based on previous studies reviewed above (Brenden et al., 2015; McParland et al., 1999; Todd and Haas, 1993) was that a sizeable (10–20%) percentage of walleyes from the Tittabawassee and Maumee rivers would move between Lake Huron and Lake Erie.

Methods

Walleye in spawning condition from adfluvial populations in Lake Huron and Lake Erie were tagged with internal acoustic tags and external Floy tags over multiple days in March–April 2011 and 2012. During the spawning period, walleye move from Lake Huron and Saginaw Bay into the Saginaw and Tittabawassee rivers (Fig. 1). The largest known walleye spawning aggregation in Lake Huron is found immediately downstream of Dow Dam (~60 km upstream of Saginaw Bay) in the Tittabawassee River (Fielder et al., 2014). Dow Dam is the first impediment to movement in the Tittabawassee River. Walleye were collected immediately downstream of Dow Dam using boat-mounted electrofishing gear.

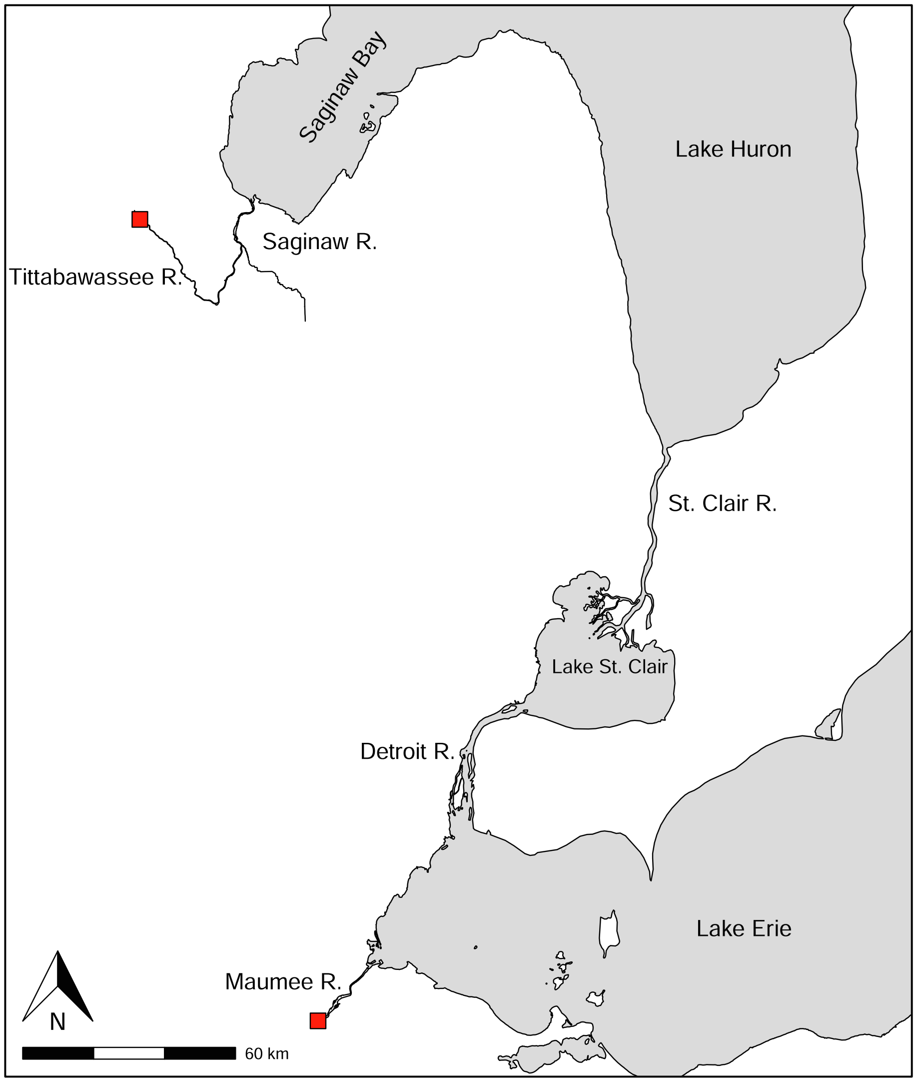

Fig. 1. Map of Lake Huron, the Huron-Erie Corridor, and western Lake Erie. Red squares indicate walleye release locations in the Tittabawassee River and Maumee River in Lake Erie. Dow Dam is located immediately upstream of the release site in the Tittabawassee River. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Located in the southwestern corner of Lake Erie, the Maumee River is the largest tributary to Lake Erie, except for the Detroit River, and supports a walleye spawning aggregation estimated at more than 500,000 individuals (Pritt et al., 2013). Walleye from the the Maumee River population were collected using boat-mounted electroshocking equipment at a location approximately 25–30 km upstream from the mouth of the Maumee River near Orleans Park in Perrysburg, Ohio. In total, 492 walleye representing the Tittabawassee River spawning population in Lake Huron and the Maumee River spawning population in Lake Erie were captured and tagged during 2011 and 2012.

Of the walleye tagged, most (399) were tagged in 2011 with nearly equal numbers tagged in the Tittabawassee (199; male = 98, female = 101) and Maumee (200; male = 103, female = 97) rivers. In 2012, an additional 60 walleye were tagged in the Tittabawassee River and 33 fish were tagged in the Maumee River. Acoustic transmitters deployed in 2011 (Vemco model V16-4H, 24 g in air, 68 mm × 16 mm dia, 1338 days of life) were programmed to emit a 152 db coded burst acoustic signal every 60–180 s (nominal – 120 s). In 2012, walleye were tagged with one of three different transmitters with similar operating specifications. Vemco V16-4H transmitters were implanted in nine walleyes captured from the Maumee River and 24 walleyes from the Maumee River were tagged with Vemco V16P-6H transmitters (98 mm × 16 mm dia, 36 g in air). In the Tittabawassee River, 39 walleyes were tagged with Vemco V16-4H transmitters, 18 walleyes were tagged with V16-6H transmitters (95 × 16 mm dia, 34 g in air), and three walleyes were tagged with V16P-6H tags. V16-6H and V16P-6H tags were programmed to emit a 152 db coded burst every 50–130 s (nominal – 90 s) and had an estimated battery life of 1844 days. All tags deployed in 2012 were recycled from tagged fish caught in the fishery, resulting in variable times-at-large in the wild that ranged from 2014 to 2017. The expected life span of tags implanted in spring 2011 was November–December 2014.

All tagging was conducted streamside near the location of capture to minimize handling time before release. Biological characteristics (sex, total length) were recorded for all fish before tagging and two external floy t-bar anchor tags (Floy FD-94; Seattle, Washington) were inserted into the anterior and posterior dorsal musculature of the second dorsal fin. Walleye were anesthetized with a portable electrosedation unit prior to surgery (PES; Smith-Root, Vancouver, Washington, pulsed DC, 35 V, 3 s treatment; Vandergoot et al., 2011). Walleye were placed in the PES exposure tank with the head oriented toward the cathode.

After immobilization was achieved, fish were placed in a cushioned foam cradle for surgical implantation of acoustic transmitters. During the surgical procedure, gills were continuously irrigated with fresh river water and acoustic tags were inserted into the coelomic cavity through a small incision located near the centerline of the ventral surface of the fish. Incisions were closed using 2–3 interrupted monofilament sutures (Ethicon PDS-II size 2-0). After surgery, each fish was immediately transferred to a recovery tank containing fresh river water until equilibrium was regained and the fish was able to swim, at which point the fish was released into the river near the capture location. On average, each surgery averaged 2.5 min and fish were released within 30 min post-surgery. All surgical tools were disinfected with a diluted solution of iodine (Cooke et al., 2011) prior to surgery. Total length ranged from 419 to 742 mm (mean = 545) for walleye tagged in the Tittabawassee River and from 450 to 781 mm (mean = 575) for walleye tagged in the Maumee River.

Omnidirectional acoustic receivers (VR2W, 69 kHz, Vemco, Halifax, NS) were deployed as part of the Great Lakes Acoustic Telemetry Observation System (http://glatos.glos.us/) in the Tittabawassee, Maumee, Detroit, St. Clair rivers and lakes Huron and Erie (Fig. 1). The number and locations of receivers deployed varied through time during 2011–2016 (Fig. 2). Receivers deployed in Lake Huron were located within ~15 km of shore and restricted to water depths less than ~40 m. In Lake Erie, the spatial coverage of the receiver network increased from receivers located in Maumee River to offshore waters of the western basin during 2011–2016 (Fig. 2). A core group of receivers (N > 20) were maintained continuously in each of the Detroit River and St. Clair River during 2011–2016. Additional receivers deployed in the Huron-Erie Corridor supported other telemetry projects.

In our analysis of between-lake walleye exchange, detections were classified into groups based on receiver deployment location. All detections from receivers in the St. Clair River and Lake St. Clair were combined (SCR; Fig. 2) and all detections from receivers in the Detroit River were combined and treated as a group (DTR; Fig. 2) for our analysis of between-lake walleye exchange. In addition to receiver groups in the Huron-Erie Corridor, detections from receivers deployed in Lake Huron and its tributaries and Lake Erie and its tributaries were combined into two separate groups for analysis. A similar receiver grouping scheme was used to characterize multi-year movement histories for all fish detected in the Huron-Erie Corridor. Receiver groups used to characterize multi-year movement histories were the same as for our analysis of between-lake walleye exchange with the exception of two additional groups that consisted of receivers located in the Tittabawassee River mouth (TTB) and Maumee River mouth (MAU). Detection of fish within spatially-defined receiver groups were used to identify movements between locations (Fig. 2). Fish movements from the Huron-Erie Corridor to lakes Huron or Erie were identified by detection of fish on receivers within Lake Huron or Lake Erie. Prior to analysis, all detections were screened for false positives caused by environmental noise and signal collisions using the short-interval criteria (Pincock, 2012). False detections were identified as detections that did not have at least one other detection from the same tag on the same receiver within 1 h. All detections that were potentially false were removed from the dataset. Ninety-nine percent of all detections in our dataset passed the false detection filter.

The probability of detecting an individual fish on an acoustic receiver can fluctuate over time and space as a result of abiotic and biotic variables in the aquatic environment (Binder et al., 2016; Hayden et al., 2016; Kessel et al., 2014). If low detection probability of acoustic tags occurs, analyses of fish movement may be biased because individuals present at the location can pass by undetected. To determine the potential scale of this problem, time-ordered pairs of detections representing movement between Lake Huron, St. Clair River, Detroit River, and Lake Erie were inspected for missed detections. Missed detections were identified as time-ordered movements between non-adjacent receiver lines. For example, detection of a walleye on receivers in the Tittabawassee River and then later in the Detroit River without a detection on receivers in the St. Clair River indicated that detection probability in the St. Clair River in-between the Tittabawassee River and Detroit River was less than one during the time period when the fish was in St. Clair River. Fish had to pass receivers in the St. Clair River prior to being detected on receivers in the Detroit River. Movements of each fish during the study revealed that all fish passing through the Huron-Erie Corridor were detected on all receivers within the Huron-Erie Corridor.

The percentage of walleye that moved into the Huron-Erie Corridor was calculated by dividing the number of walleye alive and available to be detected by the number of walleye detected on receiver lines in the Huron-Erie Corridor. These estimates were calculated separately for the St. Clair River, Detroit River, Lake Huron, and Lake Erie for 2011–2014. For a walleye that originated in Lake Huron, movement to Lake Erie was determined by detection on any receiver located in Lake Erie. Likewise, for a walleye that originated in Lake Erie, movement to Lake Huron was determined by detection of receivers in Lake Huron. Annual estimates of the number of walleye alive and available for movement to the Huron-Erie Corridor included all fish detected on any receiver in the GLATOS network and any fish not detected during a year but detected in subsequent years. If a fish was not detected in a year but was detected in subsequent years, then the fish was alive but avoided detection and was assumed to be available for movement to the Huron-Erie Corridor. The number of fish released in Maumee River that were detected in Lake Erie and the number of fish released in the Tittabawassee River that were detected in Lake Huron were not needed for our estimates of walleye movement to the Huron-Erie Corridor and were not calculated. Individual multi-year movement histories of walleye that were detected in the Huron-Erie Corridor were plotted as a function of time.

Results

Few walleyes tagged in the Tittabawassee and Maumee rivers moved into the Huron-Erie Corridor or into the alternate lake from its origin during our study, contrary to our expectations (Table 1). In the Huron-Erie Corridor, 22 walleye tagged in either the Tittabawassee or Maumee rivers were detected at least once during our study. Of these 22 walleye, 10 individuals were tagged in the Maumee River and 12 were tagged in the Tittabawassee River (Figs. 3 and 4). Most walleye (9 of 12) tagged in the Tittabawassee River that were detected in the Huron-Erie Corridor were only detected in the St. Clair River but did not enter the Detroit River or Lake Erie (Fig. 3). Of three walleye tagged in the Tittabawassee that were detected in the Detroit River, one walleye was detected on receivers in Lake Erie (Fig. 3; Tag ID 166). This fish spent less than a month during summer 2014 in western Lake Erie before returning to Lake Huron (Fig. 3). Half of the walleye tagged in the Maumee River that entered the Huron-Erie Corridor did not move upstream beyond the Detroit River (Fig. 4). Of the five fish that moved to the St. Clair River, one fish was detected on receivers in Lake Huron (Fig. 4; Tag ID 167) and two walleye returned to the Detroit River within three months after they were detected in the St. Clair River (Fig. 4; Tag IDs 343, 458). The remaining two fish (Fig. 4, Tag ID 302, 23) were only detected within the first six months after tagging, and one fish was harvested by an angler in the St. Clair River (Fig. 4, Tag ID 23). Four of the ten fish tagged in the Maumee River and seven of the 12 fish tagged in the

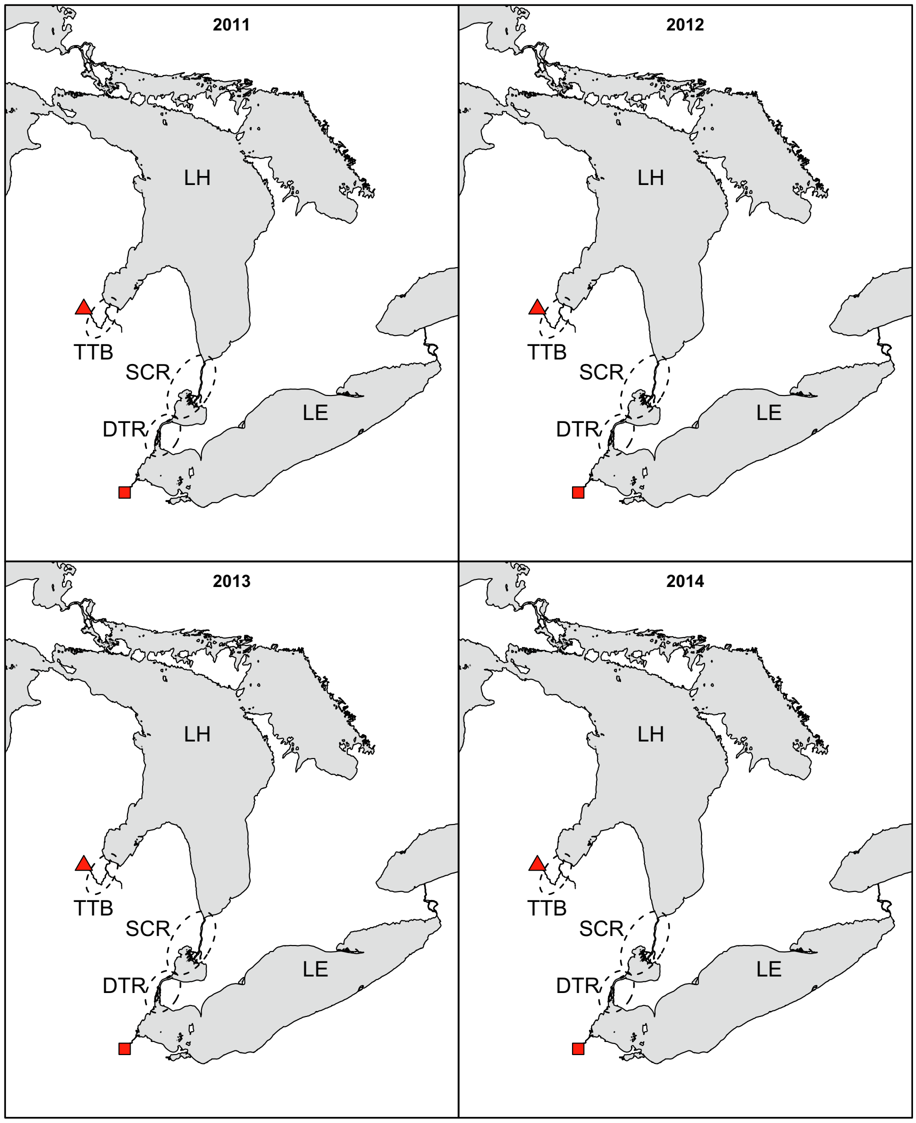

Fig. 2. Map of acoustic receiver deployments in Lake Huron, the Huron-Erie Corridor, and Lake Erie during 2011–2014. Red triangle indicates the walleye release location in the Tittabawassee River (Lake Huron) and red square is the release location in the Maumee River (Lake Erie). Each panel displays acoustic receiver locations as red circles during each year (2011–2014). Dashed ovals show receivers whose tag detections were combined for analysis in the St. Clair River (SCR), Detroit River (DTR), and Tittabawassee River (TTB). Multiple acoustic receivers deployed in the Maumee River were combined for analyses and located immediately downstream of the release site (red square). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Percentage (number in parentheses) of walleye detected on acoustic receivers located in the Tittabawassee River (TTB), Maumee River (MAU), St. Clair River/Lake St. Clair (SCR), Detroit (DTR) River, Lake Huron (LH), or Lake Erie (LE) annually (2011–2014) for fish tagged and released in the Maumee (MAU) or Tittabawassee (TTB) rivers in 2011 and 2012. The percentage of walleye tagged and released in the Maumee River that were detected in Lake Erie and the percentage of walleye tagged and released in the Tittabawassee River that were detected in Lake Huron are not reported. The total number of tagged fish alive and available for detection (N) was estimated as the sum of all fish detected on any acoustic receiver in the Great Lakes basin or any fish not detected during a year but detected in subsequent years. Walleye were captured during the spawning period, tagged with acoustic transmitters, and released near the capture location. See Fig. 2 for location of receivers.

Release	Year	TTB	MAU	SCR	DTR	LH	LE	N
MAU	2011	0 (0)	100.0 (200)	0.5 (1)	4.0 (8)	0 (0)	–	200
MAU	2012	0 (0)	80.0 (84)	1.9 (2)	7.6 (8)	1.0 (1)	–	105
MAU	2013	0 (0)	67.7 (42)	1.6 (1)	8.1 (5)	1.6 (1)	–	62
MAU	2014	0 (0)	68.1 (32)	6.4 (3)	8.5 (4)	2.1 (1)	–	47
TTB	2011	100.0 (199)	0 (0)	2.0 (4)	0.5 (1)	–	0 (0)	199
TTB	2012	95.7 (177)	0 (0)	1.1 (2)	0 (0)	–	0 (0)	185
TTB	2013	98.2 (112)	0 (0)	2.6 (3)	0 (0)	–	0 (0)	114
TTB	2014	97.3 (71)	0 (0)	6.8 (5)	2.7 (2)	–	1.4 (1)	73

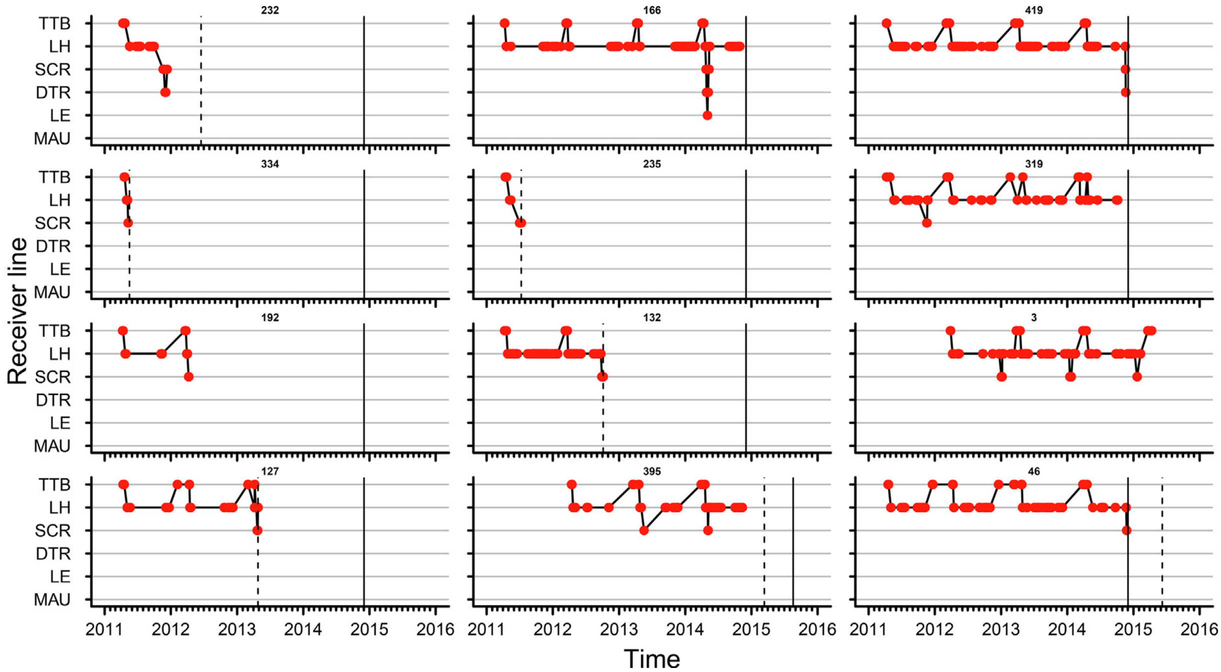

Fig. 3. Detection history of walleye released in the Tittabawassee River (TTB) that were detected on acoustic receivers in Lake Huron (LH), St. Clair River (SCR), Detroit River (DTR), Lake Erie (LE), and the Maumee River (MAU) during 2011–2016. See Fig. 2 for location of receivers. Each pane shows detections (red circles) of a single fish by location over 2011–2016. Black lines between red circles connect detections through time, and numbers above each pane uniquely identify fish. Vertical dashed lines represent the date of harvest reported by anglers and solid vertical lines were the expected end of life for acoustic tags. End of life for acoustic tag implanted in fish 3 was after January 1, 2016. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

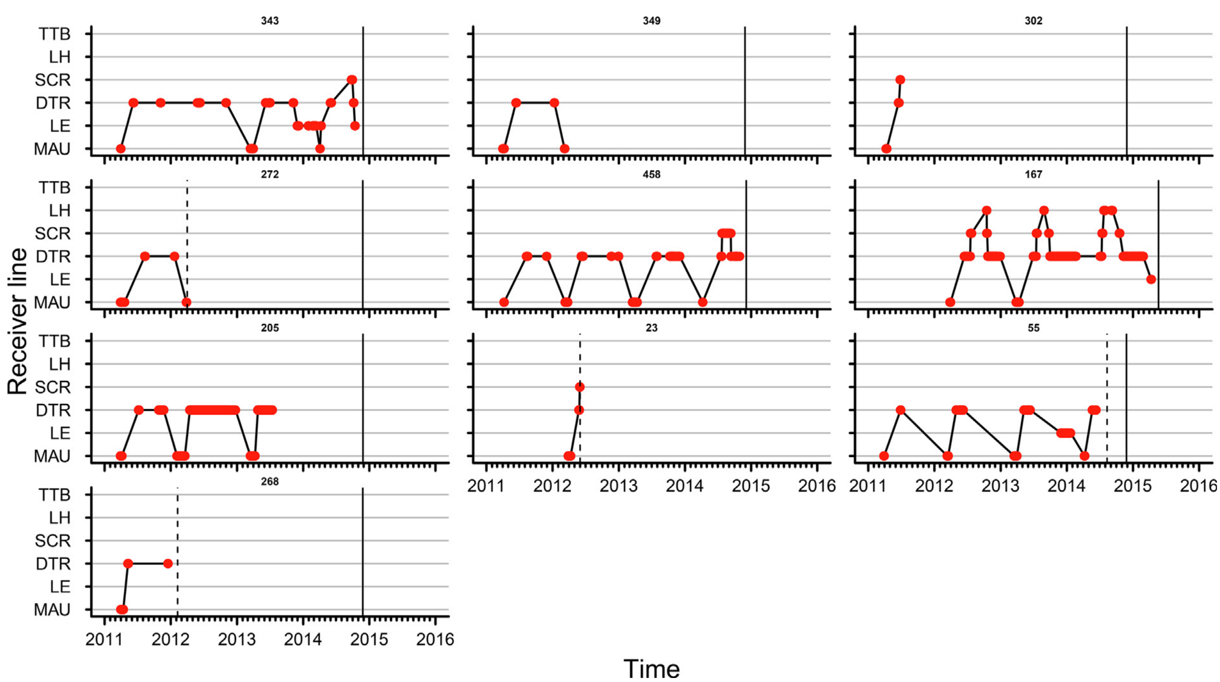

Fig. 4. Detection history of walleye released in the Maumee River (MAU) that were detected on acoustic receivers in Lake Huron (LH), St. Clair River (SCR), Detroit River (DTR), Lake Erie (LE), and the Maumee River (MAU) during 2011–2016. See Fig. 2 for location of receivers. Each pane shows detections (red circles) of a single fish by location over 2011–2016. Black lines between red circles connect detections through time, and numbers above each pane uniquely identify fish. Vertical dashed lines represent the date of harvest reported by anglers and solid vertical lines were the expected end of life for acoustic tags. End of life for acoustic tag implanted in fish 23 was after January 1, 2016. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Tittabawassee River were caught by recreational and commercial fishing during 2011–2016 based on tag returns (~50% overall exploitation rate for these migrants; Figs. 3 and 4). The last tag transmission for fish detected in the Huron-Erie Corridor on any receiver in the GLATOS network occurred prior to January 1, 2016.

The percentage of tagged fish detected in the Huron-Erie Corridor annually ranged from 0% to 8.5% (0–8 individuals – Table 1) for both release locations combined. The annual percentage of walleye that moved from the Maumee River to Lake Huron during our study ranged from 0% to 2.1% (Table 1). The number of walleye available for detection decreased over time and was lowest during 2014 for both release locations (Table 1). No fish released in the Tittabawassee River were detected in the Detroit River in 2012 and 2013 (Table 1). The percentage of walleye detected in the Detroit River from the Tittabawassee River was lower than the percentage of walleye detected in the Detroit River from the Maumee River for each year (Table 1). In contrast, the percent of walleye detected in the St. Clair River annually were similar for walleye released in the Tittabawassee or Maumee rivers (Table 1). The highest percentage of walleye detected in the St. Clair River and the Detroit River occurred during 2014 for both release locations (Table 1).

Several individual walleye showed consistent year-to-year movements into the Huron-Erie Corridor but always returned to their rivers of origin or the lake connected to the river where they were tagged (e.g., Tag IDs 3, 458; Figs. 3 and 4). Cyclic movements were more common among fish tagged in the Maumee River (7 of 10 fish) than those from the Tittabawassee River (2 of 12 fish) (Figs. 3 and 4). Detections of walleye in the Tittabawassee and Maumee rivers occurred during the annual spawning run (February–April) and walleye were detected in the Huron-Erie Corridor during summer and autumn (May–December; Figs. 3 and 4). No walleye tagged in the Tittabawassee River were detected in the Maumee River, and no walleye tagged in the Maumee River were detected in the Tittabawassee River during our study. One fish tagged in the Maumee River traveled into Lake Huron during three separate years but always returned to the Maumee River or Detroit River during the spring spawning period (Tag ID 167; Fig. 4). In each of 2012 and 2013, this fish was detected on receivers in Lake Huron for one day before it returned to the St. Clair River (Fig. 4). In 2014, this fish spent two months in Lake Huron before returning to the St. Clair River (Fig. 4).

The period of time walleye spent in the Huron-Erie Corridor varied by tagging location. Walleye tagged in the Maumee River spent longer periods of time in the Huron-Erie Corridor than fish tagged in the Tittabawassee River (Figs. 3 and 4). Walleye tagged in the Maumee River that moved to the Huron-Erie Corridor were detected multiple times over multiple weeks in the Detroit River. In contrast, walleye tagged in the Tittabawassee River were detected in the Huron-Erie Corridor only for short periods of time (<~1 week) before they were detected on other receivers in Lake Huron (Fig. 3).

Discussion

Long-term (>1 year) or one-way exchange of walleye between lakes Huron and Erie through the Huron-Erie Corridor was not observed in our study. Some walleye from Tittabawassee and Maumee rivers moved into the Huron-Erie Corridor but most left the Huron-Erie Corridor before the next spawning season. Few walleye tagged in the Tittabawassee River moved south of the St. Clair River downstream into the Detroit River, and few from the Maumee River moved upstream north of the Detroit River into the St. Clair River. Although detection of walleye movements from Lake Huron into western Lake Erie depended on receivers deployed in waters of western Lake Erie, few receivers were deployed in western or central basins of Lake Erie prior to 2013. Expansion of the acoustic receiver network in Lake Erie after 2013 decreased the probability that walleye could move undetected to offshore regions of Lake Erie from the Huron-Erie Corridor. Only Tag ID 232 (Fig. 3), a walleye from the Tittabawassee River, was detected in the Detroit River before 2013 and may have moved into Lake Erie undetected. All other walleye from the Tittabawassee River moved into the Detroit River after 2013. Past studies of walleye movement between lakes Huron and Erie via the Huron-Erie Corridor were based on fisheries-dependent recoveries of tagged walleye and did not provide information about movements by spawning populations, about individuals over multiple years, or return of individuals to the lake where tagged (Fielder, 2014; Vandergoot and Brenden, 2014; Wang et al., 2007; Wolfert, 1963). Our study is the first to directly monitor movement between lakes by population and to document movement of individual walleye into the Huron-Erie Corridor over multiple years.

Annual estimates of the percentage of walleye (0.0–8.5%; Table 1) that moved to the Huron-Erie Corridor from the Tittabawassee and Maumee rivers were similar to those from conventional mark-recapture studies. Model estimates of the percentage of fish that moved to the Huron-Erie Corridor and Lake Huron from Lake Erie ranged from 5% to 9% (95% CI) for age 5+ fish and from 8% to 14% (95% CI) for ages 2–4 (Vandergoot and Brenden, 2014). The spatially-varying population model used by Vandergoot and Brenden (2014) to estimate age-specific movement probabilities was parameterized using recapture records from more than 109,939 jaw-tagged walleye released from multiple spawning locations in US waters of western Lake Erie and tributaries between 1990 and 2007. The similarity between percentage of walleyes tagged in the Maumee River and that moved into the Huron-Erie Corridor (SCR & DTR; Table 1) in our study (4.5–14.9%) and recoveries of age 5+ jaw-tagged walleye was surprising because walleye fitted with acoustic transmitters in our study were only from the Maumee River whereas jaw-tagged walleye originated from multiple locations in Lake Erie (Vandergoot and Brenden, 2014). Annual movement rates of juvenile walleye released along the southern shore of Lake Erie to the Detroit River reported by Wolfert (3–10%) (1963) were similar to movement rates of tagged walleye to the Detroit River from the Maumee River observed in our study (4.0–8.5% Table 1), despite the fact that we tagged mature adult walleye and Wolfert (1963) tagged immature juvenile walleye. This result was surprising given that the Great Lakes have experienced substantial ecological changes in the last 50 years, and suggested that variables that influence walleye movement out of Lake Erie may not differ by reproductive status and may be temporally stable. Likewise, movement patterns of walleye revealed by nearly 100,000 walleye tagged in the Tittabawassee River during 1981–2011 (Fielder, 2014) were consistent with results of our study that suggested some walleye enter the Huron-Erie Corridor and Lake Erie. An advantage of telemetry studies over traditional tagging is the ability to track an individual's movements over multiple years while also avoiding the spatial and temporal biases caused by reliance on fishery-dependent recaptures of tagged individuals.

Walleye tagged in the Maumee River spent more time in the Huron-Erie Corridor than fish tagged in the Tittabawassee River. The difference in time spent in the Huron-Erie Corridor may reflect different motivations for moving to the Huron-Erie Corridor for these two populations. Previous work suggests walleye from the western basin of Lake Erie move eastward to cooler and deeper waters of the central and eastern basin of Lake Erie during summer (Raby et al., 2018; Wang et al., 2007). Raby et al (2018) suggested that eastward movement of walleye may be a response to water temperatures that approach thermal maximums in the western basin of Lake Erie and to obtain prey. The Detroit River is typically cooler than the western basin of Lake Erie during summer, and movements of walleye to the Detroit River may reflect a strategy for thermoregulation. In contrast, movements to the Huron-Erie Corridor by walleye tagged in the Tittabawassee River were characterized by short-duration (1 week) visits (Fig. 3). Possibly, the short-duration visits of Tittabawassee River walleye to the Huron-Erie Corridor represent exploration of new foraging areas. In a comparative study of Lake Huron and Lake Erie walleye bioenergetics, higher prey availability was attributed to faster growth of walleye in Lake Erie than Lake Huron (Madenjian et al., 2018). Given more abundant prey resources in Lake Erie compared to Lake Huron, the duration of time spent in Lake Erie by Lake Huron walleye would be expected to be higher than observed in our study if foraging was the primary motivation for movements to the Huron-Erie Corridor.

Past genetic analyses of Lake Huron and Lake Erie walleye populations (Brenden et al., 2015; McParland et al., 1999; Todd and Haas, 1993) supported our conclusion of limited permanent exchange between the Tittabawassee and Maumee populations during the spawning season, which suggested a high level of fidelity to sites of previous spawning (Hayden et al., 2018). Analyses of genetic markers from Lake Huron and Lake Erie walleye populations indicated that the Tittabawassee River walleye population was genetically distinct from Lake St. Clair and western Lake Erie walleye populations but Lake St. Clair and western Lake Erie walleye populations were not genetically differentiated (Brenden et al., 2015; McParland et al., 1999). In our study, one walleye from the Maumee River was repeatedly detected on receivers in Lake Huron; however, this fish (Tag ID 167; Fig. 4) always returned to the Detroit River or the Maumee River during the spawning season (March–April) and was not detected in the Tittabawassee River. Another walleye tagged in the Maumee River (Tag ID 302, Fig. 4) moved to the St. Clair River within 3 months of tagging. This fish was not detected during the remainder of the study (3+ years) and although we cannot definitely say that this fish immigrated to Lake Huron from Lake Erie and avoided detection, it seems unlikely that this fish was not detected on any receiver during the 3+ years before the expected end of life of its tag and possibly it was caught by the fishery. All other fish tagged in the Maumee River that were detected in the St. Clair River returned to the Detroit River after they were detected in the St. Clair River (Fig. 4; Tag IDs 343, 458, 167) or were caught and reported by anglers in the St. Clair River (Fig. 4; Tag ID 23).

An analysis of genetic structure of walleye harvested in Saginaw Bay during 2007 and 2008 suggested 26% of walleye originated in western Lake Erie or Lake St. Clair populations (Brenden et al., 2015). Brenden et al (2015) estimated that the observed composition of walleye in Saginaw Bay could be explained by a 1–2% migration rate of walleye from Lake Erie to Saginaw Bay. The goal of our study was to estimate the contribution of walleye from the Maumee River to the Huron-Erie Corridor and Lake Huron in contrast to Brenden et al. (2015) who estimated the overall contributions of Lake Erie and the Huron-Erie Corridor walleye populations to Saginaw Bay. Contributions of western Lake Erie walleye to the southern Lake Huron walleye fishery were estimated to be greater than 60% during 1994 and 1995 using allozyme and mitochondrial DNA markers (McParland et al., 1999). Estimates of the percentage of walleye that moved from Lake Erie to Lake Huron from genetic studies were substantially higher than observed in our study. Possibly our differing observations may be related to reduced immigration due to decreased abundance of pelagic prey resources in Lake Huron after 2003 (Riley and Roseman, 2013; Riley et al., 2008). Contraction of pelagic prey populations in Lake Huron may have reduced motivation for walleye to move into Lake Huron from Lake Erie. Other explanations for the observed differences between our study and results from genetic studies include contributions to Lake Huron from other Lake Erie or Huron-Erie corridor populations that were not resolved by genetic analyses or bias that resulted from non-random sampling of walleye obtained from fisheries that were used in genetic analyses (Brenden et al., 2015; McParland et al., 1999).

The exchange rate of walleye observed in our study suggested the Maumee River could not be the sole source population of Lake Erie walleye harvested in Lake Huron based on the substantial estimated contributions to the Lake Huron fisheries as suggested by Brenden et al.(2015) and McParland et al. (1999). The contribution of unknown populations represented in mixed-population genetic studies may explain the difference between our study and genetic studies. If the Maumee River population is considered independently from other western basin walleye populations, walleye movement from the Maumee River to Lake Huron averages approximately 0–2% per year as observed in our study (i.e., one fish tagged in Maumee was detected in Lake Huron) and the Maumee River walleye population is 600,000 individuals (Pritt et al., 2013), then up to 12,000 walleye from the Maumee River may move to Lake Huron annually. The Saginaw Bay walleye population was estimated to be 3 million age 2+ walleye in 2010 (Fielder and Bence, 2014). Using these values, the contribution of the Maumee River to the Saginaw Bay harvest only would be 0.4% assuming equal vulnerability between the two sources. The contribution of the Maumee River walleye population to Saginaw Bay estimated by our study is substantially less than the combined contributions of Lake Erie and the Huron-Erie Corridor to the Saginaw Bay walleye harvest estimated by genetic mixed-stock analysis (26%; Brenden et al., 2015). Possibly, the Maumee River is not the primary source of walleye immigration to Lake Huron (DuFour et al., 2015; Vandergoot et al., 2019) and other Lake Erie (e.g., Ontario and Ohio mid-lake reefs or Lake Erie tributaries) or Huron-Erie Corridor walleye populations (e.g., Lake St. Clair) also contribute to walleye populations in Saginaw Bay. Moreover, no walleye tagged in the Maumee River were detected on two parallel acoustic receiver lines at the mouth of Saginaw Bay (Hayden et al., 2014). Tagged walleye from the Thames River spawning population in Lake St. Clair tended to move north up the St. Clair River and enter Lake Huron after spawning (Ferguson and Derksen, 1971). Walleye spawning populations such as from the Thames River may contribute substantially to the Saginaw Bay walleye fishery. Additional research could identify movement patterns of walleye populations other than the Maumee and Tittabawassee rivers to determine exchange between lakes Huron and Erie, and contributions from Lake St. Clair and the Huron-Erie Corridor. Given the diversity of movement patterns observed, it is unlikely and inappropriate to assume the magnitude of exchange between lakes Huron and Erie is similar for all spawning locations in Lake Erie or Lake Huron. Combining telemetry and genetic mixed-stock analyses may be a powerful framework for resolving the relative contributions of populations in a mixed fishery (Faust et al., 2019).

Based on the results of our study, less than 0.5% of tagged walleye exchanged lakes. The corresponding binomial confidence interval (95%) for one fish out of approximately 200 tagged walleye (0.5%) that exchanged lakes observed in this study ranged from greater than 0% to 2.3%. A substantially larger sample of tagged fish than used in our study would be needed to decrease uncertainty associated with this estimate of exchange. To estimate a confidence interval (95%) with an upper bound of 1% and an exchange rate of 0.5%, more than 1000 tagged fish would be needed. In the above confidence interval calculations, we did not consider the possibility of repeated movements to the Huron-Erie Corridor or the other lake by the same fish over multiple years. We attempted to estimate movement rates while controlling for repeated observations of the same fish using binomial mixed effects models (Zuur, 2009); however, low between-lake exchange rates prevented statistical models from converging.

Management of Lake Huron and Lake Erie walleye populations are complicated by movements across provincial, state, and tribal jurisdictional boundaries, and potentially also by differing movement patterns among populations. Current management strategies that assume negligible exchange between lakes Huron and Erie are supported for management of the Maumee River and Tittabawassee River walleye populations, based on our fishery-independent results. Exchange between lakes Huron and Erie by other spawning populations are unknown and could be greater and require additional research to document. Furthermore, walleye detected in the Huron-Erie Corridor in our study returned to the lake associated with the river where originally tagged. No evidence suggested that these two populations were contributing individuals to spawning populations in the other lake, and thus these two populations do not fit a metapopulation framework where individuals from productive populations with reproductive rates that exceed mortality rates contribute to sink populations that persist because of immigration (Hanski, 1999).

The Huron-Erie Corridor is not managed independently from lakes Huron and Erie and seasonal mixing of walleye with resident populations in the Huron-Erie Corridor could result in population-specific exploitation rates. Separate harvest management strategies for the Huron-Erie Corridor could be considered if overexploitation of resident walleye populations is a concern for fisheries managers. Furthermore, repeated migrations to the Huron-Erie Corridor by individual walleye suggests that populations contain behavioral contingents characterized by different movement patterns. Thus, these contingents likely experience different vulnerabilities to harvest and thus differing fishing mortality rates that are dependent on their post-spawning movement. Behavioral contingents may increase population resiliency and stability because contingents within a population use different habitats that influence maturity, recruitment, mortality, and growth (Hayes et al., 1996; Kerr et al., 2010; Secor, 1999). Adoption of management strategies to conserve behavioral contingents of fish that move to the Huron-Erie Corridor or elsewhere may increase the resistance and resiliency of walleye populations to perturbation.

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